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Ecosystem restoration strengthens pollination network resilience and function

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Abstract

Land degradation results in declining biodiversity and disruption of ecosystem functioning worldwide, particularly in the tropics[1]. Vegetation restoration is a common tool to mitigate these impacts, increasingly aiming to restore ecosystem functions rather than species diversity *per se*[2]. However, evidence from community experiments on the impact of restoration practices on ecosystem functions is scarce[3]. Pollination is an important ecosystem function, and global pollinator declines attenuate the resistance of natural areas and agro-environments to disturbances[4]. Thus, the ability of pollination functions to resist or recover from

disturbance (i.e. the functional resilience)[5,6] may be critical for ensuring a successful restoration process[7]. We use a community field experiment to investigate the effects of vegetation restoration – here the removal of exotic shrubs – on pollination. We analyse 64 plant-pollinator networks and reproductive performance of the ten most abundant plant species across four restored and four unrestored, disturbed mountaintop communities. Restoration resulted in a marked increase in pollinator species, visits to flowers, and interaction diversity. Interactions in restored networks were more generalised than in unrestored networks, indicating higher functional redundancy in restored communities. Shifts in interaction patterns had direct and positive effects on pollination, especially increasing relative and total fruit production of native plants. Pollinator limitation was prevalent at unrestored sites only, where fruit set increased with pollinator visitation, approaching the higher fruit set levels of restored plant communities. Our results show that vegetation restoration can improve pollination, suggesting that degradation of ecosystem functions is at least partially reversible. The degree of recovery may depend on the state of degradation prior to restoration intervention and the proximity to pollinator source populations in the surrounding landscape[5,8]. We demonstrated that network structure is a suitable indicator for pollination quality, underpinning the usefulness of interaction networks in environmental management[6,9].

Main text

The loss of biodiversity has the potential to disrupt ecosystems and their functioning. Ecological restoration is often attempted to mitigate these effects[10]. Most restoration efforts target vegetation – such as the removal of exotic plants and the deliberate planting of desirable native species – in the hope that restoring the plant community

will allow other services to recover. Yet the efficacy of these interventions for restoring ecosystem functions and services has rarely been assessed quantitatively.

Pollination is an important ecosystem function, as many wild plants and crops rely heavily on pollinators for reproduction[11]. Pollinators are also particularly sensitive to anthropogenic disturbance[12,13], which poses a threat to the pollination service they provide[4]. Furthermore, restoring pollinator assemblages may be essential for ecosystem restoration. A key unanswered question is whether the common practice of restoring plant communities also leads to the restoration of pollinator assemblages and the benefits they deliver. Here we report results of a study of isolated, rocky mountaintops (inselbergs) in the Seychelles in which we experimentally assessed the effects of vegetation restoration on pollinator assemblages and their services. In particular, we quantified pollination networks and plant reproduction in both restored and unrestored communities to assess structural and functional changes in plant-pollinator communities as a response to vegetation restoration. We tested two main questions: (1) Does vegetation restoration through exotic species removal increase network interaction diversity? If so, (2) Does increase in interaction diversity in turn restore pollination function and, thus, increase reproductive output of the plant communities?

These questions are embedded in the conceptual framework that species interaction networks are key features of ecosystems[2], which makes them useful to assess the efficacy of restoration by providing comprehensive quantitative information on structure and function of communities[14]. Weighted network metrics allow us to tease

apart the influence of species abundance, diversity, generalisation, and functional overlap (Supplementary Methods 2)[15].

To account for temporal and spatial variation across a long tropical flowering season, we collected eight monthly pollination networks from eight dwarf-forest plant communities on discrete, mid-altitude inselbergs (64 networks; Fig. 1; Extended Data Table 1) on the tropical island of Mahé, Seychelles. On four of the inselbergs all exotic plants (~39,700 woody plants) were removed, referred to as 'restoration' throughout ('restored' sites; for site selection criteria see Methods and Supplementary Methods 1). The four 'unrestored' sites contained a similar number of exotic species that flowered during the study (range 2–5 spp.), accounting for 25.3 ± 15.1% of all inselberg plants. Prior to restoration, restored and unrestored sites contained a similar proportion of exotic plants (0.29 ± 0.21 vs. 0.25 ± 0.15 SD; SD hereafter unless specified otherwise; $t_6 = 0.30$, $P = 0.78$; Extended Data Table 1). After restoration, pollinators of all woody flowering plant species (38 spp.) were scored for a total of 1525 observation hours, during which we recorded 581 species-species interactions (links) and 12,235 pollinator visits to flowers. Pollinators included bees and wasps (Hymenoptera: 25 spp.), flies (Diptera: 59 spp.), beetles (Coleoptera: 38 spp.), moths and butterflies (Lepidoptera: 17 spp.), two bird species (Nectariniidae, Pycnonotidae), and three lizard species (Gekkonidae, Scincidae).

Restoration markedly changed pollinator numbers, behaviour, performance, and network structure in inselberg communities. Six to 14 months after restoration, number of pollinator species was on average 21.6% higher across the four restored compared to the unrestored inselbergs (Fig. 2). Monthly pollination networks showed

higher interaction richness and interaction diversity (a combined measure of interaction richness and evenness) in restored networks, while interaction evenness (a measure of the uniformity of the frequency of interactions) was similar between treatments (Fig. 2, Table1). Overall, restored networks were more generalised than unrestored networks (H_2', Fig. 2).

The observed network responses to restoration were mirrored by the plant communities. Most native plants were more generalised in restored than unrestored networks (d'_{pl}; Fig. 2; Extended Data Figure 1), attracting more pollinator species (Δ_{poll} = 9.0 ± 5.26 pollinator spp. on 14 of 23 plants shared between treatments). At restored sites, pollinator species were also more generalised in their partner selection (d'_{poll}; Fig. 2, Table 1). This pattern was shaped by two super-generalist and abundant pollinators, the native sweat bee *Lasioglossum mahense* (d'_{Lasio} restored vs. unrestored: 0.17 ± 0.10 vs. 0.28 ± 0.23) and the exotic honey bee *Apis mellifera* (d'_{Apis} restored vs. unrestored: 0.22 ± 0.18 vs. 0.40 ± 0.25; Extended Data Table 2), which have both been previously shown to respond most strongly to exotic plants on inselbergs[16]. Other pollinator species were also more generalised in the restored habitats (e.g. d' of endemic flies, other bees and wasps, lizards and birds; $F_{1,368.3}$ = 5.20, P = 0.023), but their effect on overall network specialisation H_2' without *Apis* and *Lasioglossum* was negligible due to their low relative abundances (d' model without *Apis* and *Lasioglossum*: treatment effect $F_{1,61}$ = 0.17, P = 0.68). Competition between exotic and native plants for pollinators played a minor role as exotics accounted for only 8.3 % (± 3.0 SE) of the total visitation frequency at unrestored sites.

More generalised networks (H_2') and species (d') at restored sites indicate greater functional redundancy and lower mutual dependencies in restored plant-pollinator communities. Greater generalisation is also associated with larger niche complementarity of pollinators and a 'sampling effect', which refers to the increased likelihood of including highly effective pollinators in a plant's pollinator spectrum[17,18]. These responses address core aims of ecological restoration: elevated functional redundancy enhances ecosystem resilience[19], lower mutual dependencies facilitate functional robustness to local species loss or decline in populations of certain pollinator species[20], and niche complementarity and sampling effect increase functional performance of the pollinator community[9,18].

The observed changes in pollinator interaction behaviour and network structure had implications for plant reproduction. Plants at restored sites produced 17.4% more flowers (floral abundance: 0.27 ± 0.037 vs. 0.23 ± 0.037 SE, Table1) and attracted 22.9% more visits (6750 vs. 5490 visits; Fig. 2), which correlated with a larger total fruit production (fruit crop) and higher fruit set (proportion of flowers producing fruit) across the most common species (Fig. 3, Table 1). The three endemic palms *Nephrosperma vanhoutteanum*, *Phoenicophorium borsigianum*, and *Roscheria melanochaetes* were among the most abundant and generalised plant species (Extended Data Table 3) and their fruit sets benefitted the most from the removal of exotics (Extended Data Figure 2). A positive relationship between generalisation and fruit production has also been observed in other island plant-pollinator communities[17], supporting the importance of super-generalist mutualists on islands[21].

149 The removal of exotic plants appeared to improve pollination, as flowers were more
150 frequently visited and native plants produced more fruit at restored sites. This
151 interpretation was supported by a positive relationship between fruit set and visitation
152 frequency (Table 1, Extended Data Figure 3). Plants at unrestored sites were likely
153 to be pollination limited, as fruit set was lower than at restored sites and increased as
154 a function of visitation, approaching similar levels of fruit set only at high visitation
155 rates (Fig. 3). Plants at restored sites had similar fruit set levels throughout the range
156 of visitation rates, possibly due to a saturating functional response of pollinators to
157 increasing floral abundance[22]. This result suggests a higher pollinator efficacy
158 compared to unrestored sites, despite the lower performance costs often associated
159 with generalist pollinator species[23]. Pollinator individuals, however, despite belonging
160 to generalist species in the networks, may respond to the higher purity of native floral
161 resources through changes in their foraging behaviour, which can result in higher
162 pollination quality[24]. Thus, one plausible explanation is that the removal of the dense
163 thickets of exotic plants enabled pollinators to detect and approach native flowers,
164 increasing visitation frequency to natives, interaction diversity, generalisation of
165 native networks and fruit set. Whether the structure and functioning of the restored
166 networks resemble those of undisturbed areas is, however, unknown, as no such
167 'reference' sites exist on Mahé.
168
169 The impact of anthropogenic habitat degradation on the structure of interaction
170 networks is well documented[25,26]. When exotic plants invade ecosystems,
171 subsequent declines in pollinator visitation, reproduction of native plants, and native
172 arthropod abundance and species richness are frequently reported[27,28]. Few studies,
173 however, have experimentally investigated community-level impacts of removing

exotic plants on biotic interactions (Supplementary Table 1). Two findings stand out: removing exotic plants may disrupt indirect facilitation of native plants, albeit on a small spatial scale, and the restoration of biotic interactions, especially of higher trophic levels, is related to time since intervention (Supplementary Table 1). Interestingly, network metrics in our study also changed over the 8-month period (e.g. number of visits increased, and H_2', d'_{pl} and d'_{poll} decreased), which may be an effect of season or time since restoration, indicated by significant main and interaction effects, respectively (Table 1). Similarly, native species diversity and abundance increased across multiple trophic levels two years after the removal of exotic plants in the Azores[29].

Previous simulation studies on woodland restoration have indicated that plant-pollinator networks undergo a succession of increasing functional redundancy and complementarity following restoration[3]. Our experiments indicate that restoration trajectories towards functionally more diverse (i.e. complementary) and robust (i.e. redundant) plant-pollinator assemblages are established as early as the first post-restoration flowering season. The prompt response to the removal of exotics may be facilitated by high 'ecological memory' in inselberg communities[30], i.e., the assemblage of functionally similar species, interactions and structures that facilitates reorganisation of an ecosystem after disturbance[5], and spatial proximity to pollinator source populations in the surrounding forest[8].

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Author Contribution

C.N.K.-B. conceived the ideas, led the experiments, collected and analysed the data and wrote the manuscript. J.M. contributed to project implementation and restoration. T.V. and R.G. conducted the restoration and collected data. A.E.W. identified pollinators. J.M.O and N.B. contributed conceptually during the planning and implementation phase. N.B. assisted with data analysis. J.M., A.E.W., J.M.O, and N.B. commented on the manuscript.

Author Information Data is available from the Interaction Web Database IWDB at https://www.nceas.ucsb.edu/interactionweb/. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to C.N.K.-B. (c.kaiserbunbury@gmail.com).

Figure legends

Figure 1| The island of Mahé with study sites and pollination networks. At each of the four restored (black circles) and unrestored (empty circles) sites we collected eight monthly networks. The webs depict bipartite quantitative networks of interactions (wedges) between plants (bottom bar) and pollinators (top bar). Each block represents a species, the width of a block reflects its relative abundance, and the width of the wedges shows the interaction frequency between pollinators and plants. Teal: Skinks and geckos, light blue: birds, dark blue: beetles, green: flies, red: wasps and bees; yellow: moths and butterflies.

Figure 2| Treatment effects on pollinator communities and network structure. Number of pollinator species (N = 8 sites; Welch's $t_4 = 3.14$, $P = 0.035$; means ± SD; data in Extended Data Table 1) and network metrics (N = 64 networks; data in Supplementary Table 2) in unrestored (U) and restored (R) plant-pollinator communities. Metrics include number of visits (Visits), number of interactions (I), interaction evenness (IE), interaction diversity (ID), network specialisation (H_2'), and plant (d'_{pl}) and pollinator (d'_{poll}) specialisation. Boxplots depict the median and ± 5%, 10%, 25% percentiles; statistics are shown in Table 1. *P < 0.05, **P < 0.01, ***P < 0.001, ns = not significant.

Figure 3| Fruit set increased with visitation rate at unrestored sites. Visitation rates (square-root transformed; N = 810 displayed seven most common species across all sites)

368 of >1.5 visits flower^{-1} hour^{-1} were only observed at restored sites. Mean fruit set was higher
369 at restored sites than unrestored sites (see Table 1 for statistics of all 10 species). Shown
370 are lines of best fit (solid) with 95% CI (dotted).

371

372 **Table 1 | Effects of vegetation restoration on plant-pollinator communities and**
373 **network structure**

(A)

Model type	Predictor	β	*t*	*P*
GLS	Number of visits (log)			
	Best model, AICcWt = 0.60, D^2= 0.14, ΔAICc = 1.72			
	Month	0.068	2.94	0.005
	Treatment	-0.305	-2.42	0.019
LM	Number of interactions			
	Best model, AICcWt = 0.51, Adj. R^2= 0.05, $F_{1,62}$ = 4.16, P = 0.046, ΔAICc = 1.95			
	Treatment	-5.500	-2.039	0.046
LM	Interaction evenness			
	Best model, AICcWt = 0.44, Adj. R^2= 0.11, $F_{1,62}$ = 8.94, P = 0.004, ΔAICc = 0.24			
	Month	-0.010	-2.990	0.004
	Alternative model AICcWt = 0.39, Adj. R^2= 0.13, $F_{2,61}$ = 5.53, P = 0.006			
	Month	-0.010	-3.013	0.004
	Treatment	-0.022	-1.406	0.165
LM	Interaction diversity			
	Best model, AICcWt = 0.42, Adj. R^2= 0.09, $F_{2,61}$ = 3.96, P = 0.024, ΔAICc = 1.31			
	Month	-0.553	-1.876	0.065
	Treatment	-2.835	-2.099	0.040
GLS	Network-level specialisation [H_2']			
	Best model, AICcWt = 0.71, D^2 = 0.27, ΔAICc = 1.84			
	Month	-0.022	-3.487	0.001
	Treatment	0.131	3.882	< 0.001

374

(B)

Model type	Random effect	Predictor	β	*t*	*P*
LMM	Crossed: Pollinator species, site	Pollinator specialisation [d'_{poll}] (N_{obs} = 703; N_{poll} = 67; N_{sites} = 8)			
		Best model, AICcWt = 0.90, $R^2_{LMM(m)}$ = 0.04, $R^2_{LMM(c)}$ = 0.22, ΔAICc = 5.74			
		Month	-0.014	-2.753	0.006
		Treatment	-0.026	-0.573	0.572
		Month × Treatment	0.021	2.997	0.003

LMM	Crossed: Plant species, site	Plant specialisation [d'_{pl}] (N_{obs} = 440; N_{plants} = 29; N_{sites} = 8)			
		Best model, AICcWt = 0.77, $R^2_{LMM(m)}$ = 0.07, $R^2_{LMM(c)}$ = 0.46, ΔAICc = 3.01			
		Month	-0.024	-4.189	< 0.001
		Treatment	0.023	0.363	0.722
		Month × Treatment	0.019	2.257	0.026
LMM	Crossed: Plant abundance (log), plant species, site	Floral abundance (log; N_{obs} = 108; $N_{Plabund}$ = 55; N_{plants} = 23; N_{sites} = 8)			
		Best model, AICcWt = 0.71, $R^2_{LMM(m)}$ = 0.02, $R^2_{LMM(c)}$ = 0.56			
		Treatment	-0.372	-2.238	0.028
GLMM (Poisson)	Nested: Branch / plant individual / plant species Crossed: Site	Fruit crop (N_{obs} = 1035; $N_{branch:indiv}$ = 159; $N_{indiv:plants}$ = 53; N_{plants} = 10; N_{sites} = 8)			
		Best model, AICcWt = 0.99, $R^2_{GLMM(m)}$ = 0.01, $R^2_{GLMM(c)}$ = 0.60			
		Treatment	-0.403	-5.147	< 0.001
GLMM (binomial)	Nested: Branch / plant individual / plant species Crossed: Site	Fruit set (N_{obs} = 1035; $N_{branch:indiv}$ = 159; $N_{indiv:plants}$ = 53; N_{plants} = 10; N_{sites} = 8)			
		Best model, AICcWt = 0.95, $R^2_{GLMM(m)}$ = 0.01, $R^2_{GLMM(c)}$ = 0.41			
		Treatment	-0.652	-3.766	< 0.001
GLMM (binomial)	Nested: Branch / plant individual / plant species Crossed: Site	Fruit set (N_{obs} = 975; $N_{branch:indiv}$ = 159; $N_{indiv:plants}$ = 53; N_{plants} = 10; N_{sites} = 8)			
		Best model, AICcWt = 0.90, $R^2_{GLMM(m)}$ = 0.02, $R^2_{GLMM(c)}$ = 0.41			
		Visitation rate (sqrt)	0.139	4.515	< 0.001
		Treatment	-0.890	-4.833	< 0.001
		Visitation rate (sqrt) × treatment	0.449	9.062	< 0.001
GLMM (binomial)	Nested: Branch / plant individual / plant species Crossed: Site	Fruit set (N_{obs} = 975; $N_{branch:indiv}$ = 159; $N_{indiv:plants}$ = 53; N_{plants} = 10; N_{sites} = 8)			
		Best model, AICcWt = 1.00, $R^2_{GLMM(m)}$ = 0.01, $R^2_{GLMM(c)}$ = 0.41			
		Visitation frequency (sqrt)	0.077	2.111	0.035
		Treatment	-0.754	-4.414	< 0.001
		Visitation frequency (sqrt) × treatment	0.358	6.229	< 0.001

Presented are statistics of the best minimal adequate models. We also showed alternative models if ΔAICc < 0.5. Full models included main and interaction effects of the predictors 'month' and 'treatment' (A; d'_{poll} and d'_{pl}), only 'treatment' (floral abundance and fruit crop and set), or 'visitation frequency/rate' and 'treatment' (fruit set). Model selection was based on AICc, and ΔAICc indicate the difference between the best and next best model. Given are also AICc weights (AICcWt) showing model probabilities. (A) Models are based on the number of networks (N = 64), assuming largely spatial and temporal independence in network parameters (see Methods). (B) Structurally more complex models with replicated sampling across species or individuals at each site include 'site' as random effect. Month

was not fitted for response variables that span the entire season (floral abundance, fruit crop and set). Coefficients of determination: adjusted R^2 (LM), D^2 (the amount of deviance accounted for by the model; GLS), and marginal and conditional $R^2_{(G)LMM}$ (R^2-equivalent for mixed models; LMM and GLMM). Restored sites were used as reference level of the factor treatment. LM = linear model; GLS = generalised least square (variance structure weighted by treatment); LMM = linear mixed model; GLMM = generalised linear mixed model; d'_{pl} = 29 native species; d'_{poll} = only bees and wasps, flies, birds and lizards with origin information.

Fruit crop refers to the number of fruit produced by the plant community at each site (conservation relevance), and fruit set describes the proportion of flowers that set fruit (ecological relevance). To assess the relationship between fruit set and pollinator visitation, we modelled two measures of visitation: weighted visitation rate (see Methods) and visitation frequency. Visitation rate (visits flower^{-1} hour^{-1}) represents the number of visits of a pollinator individual to observed flowers, i.e., a per-capita measure of pollination. Visitation frequency, calculated as visitation rate multiplied by the floral abundance of the visited plant species (see Methods), assesses the effect of community-wide floral abundance on the relationship between fruit set and pollinator behaviour.

Methods

Study sites

We collected interaction network data from eight discrete 'inselberg' (steep-sided monolithic outcrops) plant communities on the granitic island of Mahé, Seychelles, Indian Ocean (Fig. 1; Western Indian Ocean Biodiversity Hotspot) for eight consecutive months between September 2012 and May 2013 (the full flowering season; Extended Data Table 1). The eight sites constitute the majority of mid-altitude, highly diverse inselbergs on Mahé. All study sites were surrounded by steep cliffs on at least three sides of the inselberg, separating typical inselberg vegetation on the plateau from the surrounding forest, and creating comparable inselberg climate[31]. Selection criteria for inselberg study sites included elevation between 300 and 600m asl., approx. 1 ha in size, flat-topped, similar native plant communities and accessibility. Inselbergs harbour endemic dwarf-forest consisting almost entirely of perennial shrubs and small trees, forming refuges of formerly widespread woody species (Extended Data Table 3). Many inselbergs experience ecosystem degradation by encroaching exotic plant species. The most dominant exotic plants are woody perennial shrubs and trees, which are wide-spread invaders of island ecosystems, including *Psidium cattleianum*, *Chrysobalanus icaco*, *Cinnamomum verum* and *Alstonia macrophylla*. The establishment and subsequent spread of these plants on inselbergs have, however, been more gradual compared to the surrounding forest due to lower levels of human disturbance, harsh climatic, poor soils and the steep cliffs that provide a natural barrier against plant invasion. Ecological restoration, including the removal of exotic plants, is considered a suitable tool to mitigate the threat by exotic species to the long-term viability of native

ecosystems[10]. Detailed descriptions of abiotic and biotic site characteristics are given elsewhere[16,32].

To investigate the effect of vegetation restoration on plant-pollinator networks, we removed all alien plants from four inselbergs between 15 November 2011 and 10 February 2012 by cutting stems close to the ground and applying systemic herbicide to the cut stumps[33]. Treatment sites were selected to equally represent low and high degree of invasion, with each two sites per invasion level and treatment (Extended Data Table 1). Control and treatment sites were similar in plant (adonis: R^2 = 0.054, P = 0.95, Supplementary Methods 1) and pollinator communities (R^2 = 0.187, P = 0.59, data from 2007/08[16]) prior to the removal of the exotic plant species. There was no correlation between the spatial distance between sites and plant and pollinator community compositions (Mantel tests; pre-removal: plants r = 0.165, P = 0.29; pollinator r = 0.197, P = 0.32; post-removal: pollinators r = 0.231, P = 0.16), indicating no site-related inherent bias and spatial-autocorrelation between treatment levels (see also Supplementary Methods 2, Extended Data Table 4). The mean number of native plant species across sites was similar between treatments (15.0 ± 1.8 vs. 16.0 ± 2.5; Student's t_6 = -0.63, P = 0.55). Cut plant material was compiled and left to rot on site. Exotic plant removal is a widely used method in ecological restoration following the assisted natural regeneration approach[10]. This approach alters plant communities in two fundamental ways: 1) markedly reduced plant density with swaths of open habitat shortly after intervention; and 2) increased availability of resources due to reduced competition for nutrients, water and space between native and alien plants. Both alterations can affect plant-pollinator interactions directly as flowers are more easily detectable across the landscape without changes to the

453 effective distance between conspecifics[34], and native plants can allocate more
454 available resources to flowers and fruit.
455 To ensure long-term sustainability of the restoration efforts, local authorities
456 have committed to maintaining the management of exotic plants at the experimental
457 sites and incorporate inselberg habitat restoration into a national conservation
458 strategy to protect native biodiversity.
459
460 *Plant-pollinator networks*
461 To compile 64 plant-pollinator networks (8 sites × 8 months, Supplementary Table
462 2), we used established sampling protocols for focal point observations of plant-
463 pollinator interactions in heterogeneous vegetation[16,35]. Binary networks consist of
464 bars (plant and animal species) and links (interactions), in which the width of the
465 bars and links represents the abundance of flowers and animals and a measure of
466 visitation strength, respectively (Fig. 1). Flower visitors (hereafter 'pollinators'; total
467 144 spp; Supplementary Table 3) were recorded if they touched sexual parts of
468 flowers (Supplementary Methods 2). We observed all woody flowering species (38
469 spp.; Extended Data Table 3), each for 3.03 ± 0.62 hours per network. Flowers were
470 recorded monthly in 1×1×1m cubes placed stratified, randomly along several
471 transects spanning the extent of the inselbergs[16] (Extended Data Table 1). Floral
472 abundance was expressed as the number of flowers per sample cube. Pollinator
473 abundance was determined by the total number of visits of each pollinator taxon to
474 flowering plants in a network. To determine the links between plants and pollinators,
475 we calculated the *visitation frequency* between an animal species *i* and a plant
476 species *j* as mean visitation rate of animal species *i* multiplied by the floral
477 abundance of plant species *j* visited by *i*[35,36]. Visitation frequency was used to

calculate all network-level metrics (interaction richness, evenness, and diversity, H_2', d'; Supplementary Methods 2). The observation methods used here reduce the risk of under-sampling[16,37], all metrics are fully quantitative and H_2', d' are robust to sampling bias, which is pervasive in pollination network studies[38].

We calculated two distance indices to test for qualitative and quantitative differences in plant–pollinator communities within and across sites and months. Specifically, we used the Jaccard (binary) and Bray-Curtis (quantitative) indices[39] to determine species overlap and similarities in visits among networks, respectively. Species in monthly networks within sites were unique to each network by 82% (± 4.6 SD; pollinators only: 67± 4.3%; plants only: 57 ± 10.7%), and these values were similar to species uniqueness in networks across sites in given months (85 ± 1.4 %; Welch's $t_{8.4} = 1.88$, $P = 0.095$; pollinators only: 68± 3.3%, Welch's $t_{12.9} = 0.42$, $P = 0.685$; plants only: 64 ± 6.5%, Welch's $t_{11.5} = 1.58$, $P = 0.140$). Likewise, pollinator and flower communities were highly variable across sites and equally variable across months (mean Bray-Curtis distance ± SD of relative number of visits; Pollinators/site: 0.43 ± 0.09, pollinators/months: 0.46 ± 0.06, Welch's $t_{12.7} = 0.64$, $P = 0.533$; flowers/site: 0.59 ± 0.06, flowers/months: 0.63 ± 0.07, Welch's $t_{13.8} = 1.17$, $P = 0.262$). The 64 networks are therefore temporally and spatially largely disconnected, which implies a high degree of ecological independence of each network. Finally, because plant communities harboured slightly different species, we conducted all relevant analyses without native plant species that occurred only in one treatment (8 spp. marked with 'np' in Extended Data Table 3). We fitted the same models as with the full data set (see below), and the results were qualitatively equivalent and quantitatively slightly stronger than those of the entire plant communities (Supplementary Table 4).

Reproductive performance

We measured reproductive performance of native plants as the number of fruit produced at each site (fruit crop), and the proportion of flowers that set fruit (fruit set). We monitored fruit crop and set of ten native species, which occurred at two or more sites per treatment in sufficient numbers of individuals (>3 flowering females) for between-treatment comparison. Increasing total fruit crop is a restoration objective, and changes in fruit set indicate functional changes driven by pollinator behaviour and/or nutrient availability[40]. We determined fruit set of 37,898 buds on 1035 branches or inflorescences nested in 346 plants. All ten species depend mostly on pollen vectors for reproduction, as six species are dioecious or consecutively monoecious and four are self-incompatible hermaphrodites[16]. Further, eight of ten species produced fruits with one or always two seeds (*Timonius flavescens* and *Nepenthes pervillei* contained multiple seeds per fruit), thus fruit set closely corresponded with seed set.

Analyses

Analyses were conducted in R 3.1.1 (R Development Core Team; http://www.R-project.org), using the libraries *bipartite*, *vegan, lmer*, *nlme, lmerTest* and *MuMIn*. To test the response of network metrics to restoration (Supplementary Methods 2), we fitted two types of models: (1) linear (LM) and generalised least square (GLS) models without random effects, and (2) linear mixed models (LMM) with nested random terms. Network-level response variables without replication across species or individuals within a site (i.e. number of visits, number of interactions, IE, ID, and *H2'*) were fitted with LM or GLS (Table 1A), depending on the variance structure.

When heterogeneity was detected we used the *varIdent* function with GLS models to assign weight to the variance by the treatment stratum[41]. We analysed species-specific responses of plant (d'_{pl}) and pollinator specialisation (d'_{poll}) and floral abundance to treatment with linear mixed models (LMM). These response variables contain data on within-site variation across species, we thus fitted species and sites as crossed random effects, and month (only d') and treatment (all) as fixed effects (Table 1B). LM and GLS were based on the number of networks (N = 64), treating each network independently. The following rationale warrants the analytical approach: eight study sites may be considered statistically too low to detect ecologically meaningful results despite the extent of the ecosystem-level field experiment. To avoid an inflated 'type I error', we repeatedly sampled highly dynamic interaction networks over time. We showed that the composition of plant and pollinator communities in the networks was highly variable within and among sites and months (see above), suggesting a low degree of overlap between networks from the same site and month. Further, each observation session focussed on a different plant individual, which ensured within-site spatial separation between consecutively observed interactions. Finally, support for our approach comes from the visual inspection of partial residual plots, which depict treatment effect after removing the effects of time (fixed effect) and site (random effect in LMM; Extended Data Figure 4). We therefore considered networks independently for structurally simpler models on network metrics (number of visits, number of interactions, IE, ID, and *H2'*, Table 1A) and fitted LM and GLS models with the fixed main effects month and treatment and the interaction between month and treatment. The best model was selected with the *dredge* function (package: *MuMIn*) based on AICc. AICc weights are presented to indicate the level of support for selecting the most parsimonious among

553 a set of models. ΔAICc assesses the support of the best and second best models,
554 and alternative models were shown only when ΔAICc < 0.5 (Table 1). Given are also
555 AICc weights (AICcWt) showing model probabilities[42]. We computed the adjusted R^2
556 D^2, and marginal and conditional $R^2_{(G)LMM}$ as goodness-of-fit metrics for linear,
557 generalised least square, and mixed models, respectively. D^2 is the amount of
558 deviance accounted for by the model[43], and marginal and conditional $R^2_{(G)LMM}$ are
559 coefficients of determination for mixed models describing the proportion of variance
560 explained by the fixed factors only (marginal $R^2_{(G)LMM}$) and by both the fixed and
561 random effects (conditional $R^2_{(G)LMM}$)[44]. To test the influence of seasonality we ran
562 models initially with each one of three time effects: linear across months, a quadratic
563 term to reflect a hump-shaped seasonality, and a factor with eight levels. All models
564 showed a poorer (> AICc) fit of the quadratic term and the factor compared to the
565 linear fit. We therefore fitted in all models the linear time effect.
566 Treatment effects on total fruit crop and fruit set were tested with generalised
567 mixed models (GLMM) with Poisson and binomial distributions, respectively. To
568 account for unbalanced data and spatial and within-species dependencies, we used
569 species (in the model containing all species), plant and branch identity as nested and
570 site as crossed random effects. In the binomial models, we also weighted sample
571 sizes by the number of flowers recorded on each plant to calculate fruit set (*cbind*
572 function). Fruit set was also tested for each species separately (Supplementary
573 Methods 3, Extended Data Figure 2). To assess the functional relationship between
574 fruit set as a proxy for plant reproductive performance and pollinator behaviour, we
575 calculated weighted visitation rate and used a reduced fruit data set containing only
576 those species that were visited by pollinators in a given network (N = 975). Visitation
577 rate represent the number of visits of a pollinator individual to observed flowers,

578 expressed as rate of visits flower^{-1} hour^{-1}. Weighting was achieved in two steps: first,
579 because dioecious palms attracted a large proportion of visitors to either male or
580 female flowers, we considered the distribution of pollinator species between sexes in
581 a weighted visitation rate (*VR*) as follows:

$$VR = \sum_i v_i \cdot \frac{2 \cdot \min(m_i, f_i)}{m_i + f_i} flower^{-1} h^{-1}$$

582 where v_i is the total number of visits of pollinator *i;* m_i and f_i are the number of visits
583 to male and female flowers, respectively, visited by *i* in the network. This approach
584 ensures that pollinators with equal visits to male and female flowers are fully
585 weighted (ratio = 1) whereas pollinators that only visit one sex are not considered
586 (ratio = 0). The second step incorporated the importance of a pollinator species for a
587 plant species by dividing weighted visitation rate by the total sum of all visits. The
588 same steps were repeated with visitation frequency to assess the influence of
589 community-wide floral abundance on the relationship between fruit set and pollinator
590 behaviour (Extended Data Figure 3).

591 **References Methods**

592

593

Extended Data tables

Extended Data Table 1 | Study site details and summary of plant and pollinator communities

Extended Data Table 2 | Results of full-factorial linear mixed model. Comparison of species-level specialisation d'_{poll} (log-transformed) between species (the exotic honey bee *Apis mellifera* vs. the native sweat bee *Lasioglossum mahense*) and treatments (restored vs. unrestored). Site was entered as a random effect. Numbers in bold are significant at $\alpha \leq 0.05$.

Extended Data Table 3 | List of plant species included in the study

* The following species were recently renamed: *Diospyros boiviniana* = *Maba seychellarum; Polyscias crassa* = *Gastonia crassa; Pyrostria bibracteata* = *Canthium bibracteatum; Peponidium carinatum* = *Canthium carinatum*; † LC = least concern, NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered; - = exotic species, not listed. ‡ across all networks [sum of number of flowers/cube across the eight sites]; § Equals number of interactions, na = not applicable, np = not present; ‖ R = restored sites; U = unrestored sites; bold font indicates species included in reproductive performance analysis (fruit crop and fruit set)

Extended Data Table 4 | Spatial auto-correlation coefficients of community and network parameters across the study sites. Numbers in bold are significant at $\alpha \leq 0.05$.

Extended Data figures

Extended Data Figure 1| Level of specialisation (d'_{pl}) of the 10 most common flowering plant species across all networks. Asterisks (*) indicates a significantly higher level of specialisation (mean ± SE) in the unrestored compared to the restored networks. For full

621 species names see Table 3. Linear mixed model: *P. bibracteata* t = 2.836, P = 0.036; *P.*
622 *lancifolia* t = 2.644, P = 0.038; *E. sechellarum* (variance structure weighted by treatment) t =
623 3.141, P = 0.020. Site was entered as random effect in all models. All other species $P >$
624 0.05.
625
626 **Extended Data Figure 2**| **Fruit set of the ten most abundant plant species.** The species
627 occurred at ≥ 2 sites per treatment (*Nepenthes, Mimusops*), seven sites (*Roscheria*,
628 *Timonius*), and eight sites (all others). The reproductive systems included dioecy (*Pyrostria,*
629 *Nepenthes, Timonius*), monoecy with temporally separated male and female flowers
630 (*Roscheria, Phoenicophorium*, *Nephrosperma*) and protandrous hermaphrodite flowers
631 (*Erythroxylum, Memecylon, Mimusops, Paragenipa*). The three palm species *Roscheria*,
632 *Phoenicophorium* and *Nephrosperma* had higher fruit set at the restored sites (GLMM:
633 *Nephrosperma* N = 120, z = 2.54, P = 0.011, *Phoenicophorium* N = 120, z = 2.66, P = 0.008,
634 *Roscheria* N = 108, z = 2.29, P = 0.022), the other species showed no clear species-specific
635 pattern. The boxes depict the median and 25th and 75th percentiles, whiskers show 1.5 ×
636 interquartile range of the data, and open circles indicate outliers.
637
638 **Extended Data Figure 3**| **Fruit set increased with visitation frequency at unrestored**
639 **sites**. Square-root-transformed visitation frequency (N = 810, displayed seven most
640 common species across all sites) of >1.5 visits flower^{-1} hour^{-1} × floral abundance were only
641 observed at restored sites. Mean fruit set was higher at restored sites than unrestored sites
642 (see Table 1 for statistics for statistics of all 10 species included in reproductive performance
643 analysis). Shown are lines of best fit (solid) and 95% CI (dotted).

644 **Extended Data Figure 4**| **Partial residual plots of network metrics**. Box plots of partial
645 residuals show the effect of treatment after removing the effect of month and site. Partial
646 residuals were calculated from linear mixed models with month and treatment as fixed main

and interaction effects and site as random effect. Shown are partial residuals plus intercept. Boxplots depict the median and ± 5%, 10%, and 25% percentile.